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# ON THE SYSTEMATIC POSITION OF *MACELOGNATHUS VAGANS*

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## ABSTRACT

The holotype and only known specimen of *Macelognathus vagans* was placed in a separate reptilian order (Macelognatha) by O. C. Marsh in 1884. Restudy of the specimen and of other extensive collections from the *Macelognathus* site (Quarry Nine, Como Bluff, Wyoming) and a careful check of Peabody Museum records suggest that *Macelognathus* probably belongs to the Order Crocodilia.

## INTRODUCTION

The peculiar specimen described here (see Figure 1) was, and still is, the sole basis for a "new" order of reptiles proposed by O. C. Marsh in 1884. Marsh suggested that his new Order Macelognatha was most closely "allied to the Chelonia" (1884, p. 341), but the few authors who have cited *Macelognathus* subsequently have usually referred it to one or another of the dinosaurian suborders. Uncertainty about its proper systematic position stems from the unique combination of a normal series of tooth sockets along the rear portions of the dentaries coupled with a strange, spatula-shaped, toothless anterior extremity of the lower jaws. The principal paleontologic references at the turn of the century (Nicholson and Lydekker, 1889 and von Zittel's text, various editions from 1890 on) cited *Macelognathus*, but subsequently it has been omitted (presumably because of its uncertain identity) from all modern texts and references<sup>1</sup> with the exception of von Huene's (1956) *Paläontologie und Phylogenie der Niederen Tetrapoden*. At present, *Macelognathus* is still of uncertain affinity.

Considering the extremely rich and diverse collections of Jurassic fossil vertebrates obtained from Quarry Nine, Como Bluff, Wyoming—the site of *Macelognathus*—as well as the extensive exploration and collecting from the Morrison Formation since 1884, it seems most improbable that no other fossil remains pertaining to this taxon exist. The present paper summarizes a recent search for such evidence and suggests a new systematic position for this enigmatic specimen.

## TAXONOMIC HISTORY

*Macelognathus vagans* was founded on two incomplete dentaries (YPM 1415) by Marsh (1884) in a very brief description supplemented by a single illustration. Marsh described the specimen as:

two dentary bones of the lower jaws. These bones resemble in many respects the corresponding parts of a turtle, but are broader, and more nearly horizontal. The jaws were evidently covered with a horny beak in front, but further back they contained teeth. The edentulous portion is flat and thin, and nearly horizontal. The two rami meet in nearly the same plane, and are united at the symphysis by a close suture. . . . The teeth were implanted in distinct sockets, in front, but further back, the walls between them become thinner, and a groove appears to gradually take their place. The form of the teeth cannot be determined from the present specimen. (1884, p. 341).

1. Romer (1966) lists "*?Marcellognathus* U. Jur. NA" under Hypsilophodontidae, Suborder Ornithopoda, but it is not known whether or not this citation refers to the specimen under consideration here.

Marsh's assessment of *Macelognathus* relationships was that:

These jaws are too solid and massive for Birds or Pterodactyles. With Serpents and Lizards they have evidently only remote affinities. The close union of the rami by suture separates them from the Dinosaurs, and the edentulous beak, from the Crocodiles. They appear to be nearest allied to the Chelonia, although Turtles without teeth occur in the same strata with them. (1884, p. 341).

Nicholson and Lydekker (1889) suggested that *Macelognathus* may possibly represent a generalized family in the Suborder Athecata—the most generalized turtles that show approximation to other reptiles. Karl von Zittel, on the other hand, assigned *Macelognathus* to the Family Stegosauridae (Suborder Predentata, Order Dinosauria) in the 1890 edition of his textbook. In 1891, George Baur, a former student of von Zittel's and a then recently resigned assistant to O. C. Marsh, published an important critique on the validity of the Order Dinosauria (his conclusion was that it did not represent a natural group) in which he included a footnote "I think that *Macellognathus* [sic] Marsh, which has nothing whatever to do with the Testudinata, belongs to this family [Coeluridae] and to *Coelurus*." (1891, p. 450). Unfortunately Baur never published his reasons for this conclusion.

Marsh (1897) referred to *Macelognathus* once more and refigured it, but did not comment further on its taxonomic position. O. P. Hay (1902) stated incorrectly that Marsh placed *Macelognathus* in the Testudinata but then placed it in the (then debateable) Order Dinosauria with the qualification that its phylogenetic relationships are problematical. Subsequent authors have assigned it without explanation as follows: Moodie (1908)—Dinosauria; Gilmore (1909)—Reptilia; Mook (1916)—Reptilia; Simpson (1926)—Ornithischia; von Huene (1956)—Ornithischia (Hypsilophodontidae). In 1966, Strom and McIntosh referred this specimen questionably to the Crocodilia or Eosuchia.

#### HISTORY OF THE SPECIMEN

Peabody Museum records show that the holotype of *Macelognathus vagans* was collected by William Reed during the summer of 1880 from Quarry Nine, the famous mammal quarry at Como Bluff, Wyoming. It, together with numerous other specimens, was shipped in two boxes (Nos. 75 and 76) to Yale and was received and accessioned (No. 1394) on Sept. 18, 1880. Accession number 1394 was applied to all the contents of both boxes. The accession entry for box 75 reads "Containing one box of cans from Quarry 9, (Box 75½) inside of Box 75, and balance from [Quarry] 13 W. and four packages from west side of middle gulch." A series of notebooks in the Peabody Museum archives gives further details on the collections received from Marsh's

collectors. One such notebook compiled by Otto Meyer, one of Marsh's assistants, is dated 1884 and entitled "Notes on Jurassic vertebrates from Quarry 9, Como, Wyom." It records in some detail the contents of several dozen boxes and cans accessioned from Quarry Nine. Accession No. 1394, as applied to the contents of box 75½, is recorded on five separate pages under five different entries—numbers 1 to 5. This presumably indicates that the contents consisted of five separate packages (cans, according to the accession entry), if other accession entries in this notebook and in other Museum records are accurate. Only two references to lower jaws are recorded in Meyer's notes under accession number 1394, "lower Jaws" (plural), unidentified, listed under package No. 3 and "lower jaw" (singular), identified as crocodile, listed under package No. 4. A single crocodilian mandible with accession number 1394 still resides in the Peabody Museum collections and this almost certainly is the jaw listed under No. 4 in Meyer's notebook. Accordingly, it appears most probable that the unidentified lower jaws listed under No. 3 are those now referred to as *Macelognathus vagans* (YPM 1415).

The information recorded in Meyer's notebook takes on special significance when it is realized that Marsh was most particular in his instructions to all of his collectors. He required every collector to be meticulous in collecting procedures and in preserving and recording specimen sources and associations (see his directions for collecting vertebrate fossils, p. 172–173 in Schuchert and LeVene's biography of Marsh). Moreover, Reed was an experienced collector who had worked for Marsh as one of his most trusted field men since 1877. In the light of this information, it seems safe to assume that the material packaged with the unidentified lower jaws and recorded by Meyer as No. 3 represents fossil remains that were closely associated in the quarry. That these other materials actually belonged to the same individual as the jaws is beyond proof, of course, but their relevance to the identity of *Macelognathus* cannot be dismissed. In addition to the unidentified jaws, Meyer listed "sorted teeth" (unidentified) and a scute, calcaneum, cuboid, neurapophysis of an atlas, and a metatarsal—all identified as crocodile. Opposite these crocodilian items Meyer wrote "Note. These bones resemble more the corresponding ones in the *young* alligator, than in the old one." Although a variety of turtle, lizard and dinosaurian remains were also accessioned with *Macelognathus*, Meyer's notes clearly record that only crocodilian remains were packaged (and thus probably closely associated in the quarry) with this specimen.

A thorough search of the Quarry Nine collections in the Peabody Museum at Yale turned up a tray with accession number 1394 containing "sorted" teeth and crocodilian remains that match in part Meyer's description (a neural arch, a scute and a metatarsal) plus a note in Marsh's handwriting stating "*Macelognathus* jaws taken from here March 22nd, 1884, OCM." Although the "cuboid" and "calcaneum" have not been recognized they may be represented among the several small fragments in the tray. The scute, neural arch, metatarsal and teeth are clearly crocodilian. These have been catalogued as YPM 5539.

REVISED DESCRIPTION

*Macelognathus* Marsh

*Macelognathus* Marsh, 1884.

TYPE SPECIES. *Macelognathus vagans* Marsh, 1884.

TYPE SPECIMEN. YPM 1415, symphyseal and anterior portions of left and right dentaries, figured by Marsh (1884, p. 341 and 1897, figs. 65, 66).

TYPE LOCALITY. Quarry Nine, SW 1/4 Sec. 12, T. 22 N., R. 77 W., Como Bluff, Albany County, Wyoming.

DESCRIPTION. When placed in articulation the two dentary fragments form a shallow, spatula-like symphyseal extremity, the anterior portion of which was edentulous. The symphysis is long and shallow and with very low inclination almost parallel to the mandibular axis. The symphysis itself measures  $47 \pm$  mm in length with a maximum depth (perpendicular to length) of 9.0 mm. The symphysis appears to have been a straight, strongly digitate suture that provided a strong and relatively immobile union of the two mandibles. There is, however, no evidence of fusion between the jaw rami. A narrow medial groove, the rostral extension of the Meckelian canal, marks the long axis of each symphyseal suture in their posterior halves, quite similar to the condition in modern crocodilians.

The width across the articulated dentaries at the anteriormost alveoli (approximately 35 mm behind the anterior extremity) is 41.5 mm. The anterior margins are no longer intact, but the little that remains indicates a very thin, sharp-edged, perhaps slightly denticulate rostral margin comparable to the figures published by Marsh (1884, 1897). The posterior extremities are missing from both fragments, consequently no accurate estimate is possible for the original dentary (or mandible) length. Neither fragment preserves any evidence of reduction in either height or thickness along the posterior region, but judging from the sizes of the tooth sockets, I would estimate that the present fragments represent less than half of the original dentary length. The greatest preserved length of the two *Macelognathus* fragments is slightly more than 10 cm.

Eleven alveoli are preserved in the left dentary fragment extending over a distance of 67 mm. Nine alveoli are at least partially preserved in the right fragment over a length of 59 mm. Not all alveoli are equally distinct, but most show a concave outer wall and a straight or slightly concave inner wall. Inter-alveolar bony walls are preserved in the right dentary, but are poorly preserved or missing in the left. Alveolar dimensions vary, but most approximate 5 to 6 mm in longitudinal and about 4 mm in transverse dimensions. The alveoli all appear to be relatively deep sockets. Both dentaries lack teeth entirely and it is this deficiency, together with the peculiar, toothless rostrum, that has made placement of this specimen so uncertain. Several tooth sockets

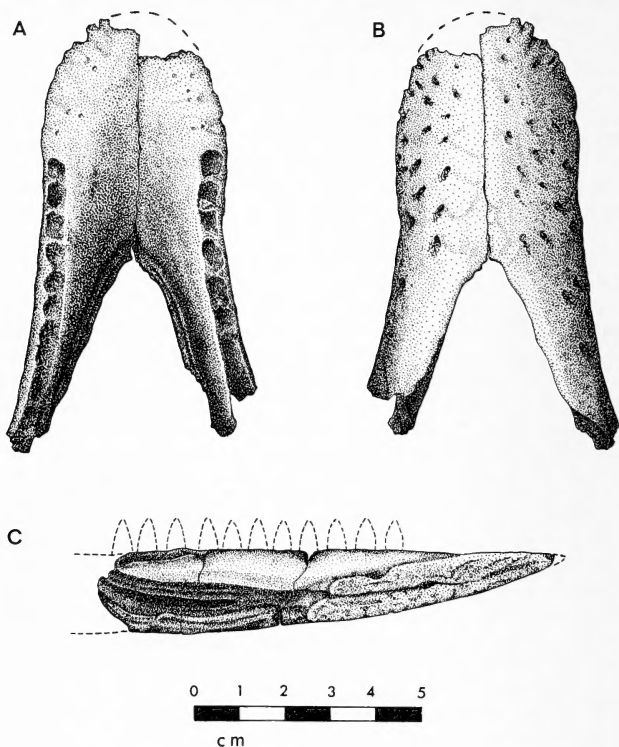


FIG. 1. Holotype of *Macelognathus vagans* (YPM 1415) in dorsal (A) and ventral (B) aspects. Medial view of the left dentary (C) shows the elongated and shallow symphyseal suture, and the "splenial facets" on the inner surface.

were excavated for tooth fragments and both dentaries were X-rayed for evidence of replacement teeth. These efforts were to no avail. Both dentary fragments are undistorted and show a pronounced change in alveolus orientation from the front of the tooth row to the back. The anteriormost alveolus on each side is inclined at about  $45^\circ$  to the sagittal plane, whereas the most caudad sockets appear to have had a more nearly vertical orientation. This condition is not diagnostic of crocodilians, but it is present in *Alligator* and *Crocodylus*.

The lateral and ventral surfaces are not sculptured, but they are marked

by numerous widely spaced foramina of small to moderate size that seem to radiate away from the symphysis. There are faint grooves or channels associated with some of these. This surface texture is distributed over the dentary surfaces immediately adjacent to the tooth row as well as on the anterior toothless region. Marsh (1884) suggested that the anterior portions of these jaws were covered with a horny beak and such may have been the case, but microscopic examination failed to reveal any evidence of this. The dentaries of *Macelognathus* show no conspicuous change in surface texture or in foramina density between the anterior toothless region and those surfaces adjacent to the tooth row. By contrast, those parts of turtle mandibles that are covered by horny beak are much more highly perforated than those parts that are not so covered. It seems very unlikely to me that both the toothed and toothless regions alike were enclosed in a horny beak. Furthermore, the density of foramina is considerably greater in turtle mandibles than it is in *Macelognathus*. In fact, the surface texture and pattern of foramina in *Macelognathus* are very different from those of turtle jaws, but they are almost identical to those found in this region of Recent *Alligator* and *Crocodilus*. These facts indicate that the jaws of *Macelognathus* were covered by normal epidermal tissues rather than a horny beak.

The medial dentary surfaces are marked by broad and moderately deep Meckelian canals that narrow anteriorly and lead into the medial symphyseal groove mentioned above. In both fragments, the Meckelian canal is bordered above and below by shallow but distinct grooves or facets. The superior groove extends to within about 12 to 14 mm of the symphysis, but the inferior grooves appear to reach all the way to the symphysis. These surfaces are believed to be the articular surfaces for the splenials and as such indicate that the splenials probably contributed to the symphyseal junction. This condition may be significant for the systematic placement of *Macelognathus*.

#### SYSTEMATIC POSITION OF *Macelognathus*

Chelonian affinities of *Macelognathus*, sometimes attributed to Marsh, can be dismissed on several grounds; these include the presence of well-defined alveoli indicative of a thecodont dentition, the unfused symphysis, the apparent junction of the splenials at the symphysis, the flat and rounded symphyseal region rather than a sharp, triangular beak, and the surficial textural evidence of a closely applied, epidermal covering rather than a horny beak. Ornithischian affinities appear improbable because there is no evidence whatsoever of a predentary—the anterior, medial mandibular element that is present in all adequately known ornithischians. Moreover, the symphysis in all ornithischians is short and weakly developed, apparently forming a mobile union, and the splenials terminate far posterior to the symphysis. Baur's unexplained reference of *Macelognathus* to the Coeluridae (Order Saurischia) is not substantiated by comparison with any known theropod, a group in which the symphysis is universally short and apparently flexible, and the splenials are

short and fail to meet at the symphysis. Rhynchocephalian remains have been collected at Quarry Nine, but the thecodont tooth implantation of *Macelognathus* rules out any close relationship with this order. Squamatan affinities appear remote on the basis of the relatively large size of *Macelognathus* and the firm symphyseal junction involving the splenials.

Splénial involvement in the mandibular symphysis is characteristic of a number of long-snouted reptiles (i.e. Mesosauria, Ichthyosauria, Sauropterygia, Phytosauria, Eosuchia and some crocodilians including living gavials<sup>2</sup>) and is not necessarily consistent among closely related taxa. In all instances splénial symphyseal articulation is correlated with elongation of the symphyseal suture and does not appear to be necessarily related to anterior elongation of the splenials. Symphysis elongation presumably is related to snout elongation or immobilization of jaw symphysis. This correlation of symphysis elongation and splénial junction apparently holds true for *Macelognathus*.

Of the groups mentioned above, only the eosuchians (and specifically the champsosaurs) and crocodilians are serious candidates for consideration as relatives of *Macelognathus*. Initially, I suspected that YPM 1415 might represent an early member of the Choristodera, largely because the splénial symphyseal junction is so extensively developed in all known champsosaurs. My suspicion appeared to be reinforced by a recent discovery by a Princeton University expedition of a very similar spatula-mouthed champsosaur from the Paleocene of the Big Horn Basin in Wyoming (D. Baird, pers. comm.). However, after further consideration and extensive examination of the Morrison fauna, I have come to the conclusion that *Macelognathus*-champsosaur affinities are highly improbable and crocodilian relationships are much more likely.

A very thorough search during the last four years through all of the collections from Quarry Nine that are housed in the Peabody Museum and in the United States National Museum failed to turn up a single piece of evidence to corroborate *Macelognathus*-champsosaur relationships. Every tooth, jaw and vertebra from Quarry Nine (of which there are several thousand) was examined, as was a large number from other quarries at Como Bluff. Despite the distinctive character of champsosaur teeth and vertebrae, not a single item was found that even remotely resembled these elements as they are presently known in the Choristodera. Negative evidence is seldom conclusive, but the extraordinary abundance of material available from this classic site, and its great diversity, makes it highly improbable that other remains of *Macelognathus* are not represented in the collections from Quarry Nine. Failure to discover recognizable champsosaur remains in the Quarry Nine collections or in any other Morrison collections can hardly be considered proof of non-choristoderan relationships. It is quite possible that early choristoderans had not yet acquired the distinctive vertebral or dental characters of champsosaurs.

2. Langston (1965), reported a supposed Miocene gavialid in which the splénial makes a large contribution to the symphyseal suture.

But, on the other hand, crocodilian remains are very abundant in the Morrison Formation, and especially so in the Quarry Nine collections. Moreover, they constituted the only recognizable remains packaged with the specimen in question, as well as constituting the most abundant remains accessioned under 1394.

The evidence is largely circumstantial, but the only anatomical feature preserved in YPM 1415 that is not presently known in the Crocodilia is the edentulous, spatulate rostrum. I suggest that the total evidence now available indicates a crocodilian relationship for *Macelognathus*.

#### SUMMARY

Reassessment of Museum records, probable quarry associations, the Quarry Nine fauna and the morphology of the holotype and only known specimen of *Macelognathus vagans* (YPM 1415) indicate that the most probable affinities are with the Order Crocodilia and not with turtles or any dinosaurian group. Thecodont dentition, long symphyseal suture, splenial participation in the symphysis, and the evidence of epidermal rather than horny covering of the mandibles are consistent with crocodilian relationships.

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